

NEST PREDATION IN FRAGMENTED FORESTS: LANDSCAPE MATRIX BY DISTANCE FROM EDGE INTERACTIONS

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ABSTRACT.—Forest fragmentation due to forestry management, agricultural activities, or urban development decreases habitat availability for some animals. This decline in forest area has been implicated in songbird population declines via changes in nest predation pressures. The increase of edge habitat that accompanies deforestation also may affect songbird breeding activities through changes in predation risk. This study found evidence for an interaction effect of distance from edge (1, 15, 30, and 45 m) and adjacent landscape matrix (residential or forested) on nest predation rates using an artificial nest design. In fragments bordered by other forested patches, nest predation rates were lowest 1 m from the edge and higher 15–45 m into the forest patch. When the forest fragment was embedded in a landscape matrix of residential and developed plots, predation rate was highest closest to the edge of the fragment. Received 28 August 2000, accepted 13 March 2002.

Accumulating evidence suggests that many Neotropical migrant songbirds are experiencing drastic population declines (Terborgh 1989). Forest-nesting birds are challenged by loss of breeding habitat, fragmentation of breeding habitat into smaller and smaller forest patches, and changes in the landscape surrounding these forest patches. These habitat changes can have a myriad of effects on forest nesting species (Hagan and Johnston 1992). Population density may increase immediately upon forest fragmentation, leading to increased competition for suitable nest sites and prey items (Hagan and Johnston 1992, Van Horn et al. 1995, Hagan et al. 1996, Holmes et al. 1996). Cowbird parasitism may increase (Terborgh 1989). Predator community composition may change, resulting in increased rates of nest predation (Bider 1968, Gates and Gysel 1978).

Nest predation is a major cause of reproductive failure in birds (Ricklefs 1969), and changes in nest predation rates may cause the disappearance of sensitive bird species from fragmented landscapes. Results from numerous studies consistently have demonstrated that nest predation rates increased as forest fragment size decreased (Wilcove 1985, Møller 1988, Small and Hunter 1988, Yahner and Scott 1988, Paton 1994, Hoover et al. 1995, Hartley and Hunter 1998, Keyser et al.

1998). However, it is less clear whether this effect resulted from decreased core forest area *per se* or from increased amount of edge habitat.

Edges are transitional zones from one habitat type to another. They are characterized by abiotic and biotic features distinct from the habitats on either side of the edge. For example, increased sunlight and wind exposure at edges often change the plant species composition at edges. Edge effects have been implicated in songbird population declines, and several studies have attempted to document edge effects on nest predation rates. However, the results of these studies have been contradictory (e.g., Gates and Gysel 1978, Yahner and Wright 1985, Angelstam 1986, Andrén and Angelstam 1988, Small and Hunter 1988, Møller 1989, Linder and Bollinger 1995, Hanski et al. 1996, King et al. 1996, Keyser et al. 1998). This lack of consistency may be due to problems of experimental design (Paton 1994, Murcia 1995). In many studies, the landscape matrix surrounding the forest fragments was not considered; however, the few studies that did measure nest predation relative to surrounding landscape characteristics found them to be very important (Andrén and Angelstam 1988, Andrén 1995, Donovan et al. 1997). Edge effects also may be confounded by the effect of forest fragment size. Finally, many researchers expect a monotonic relationship between distance from edge and nest predation rates. Few artificial nest studies have used nests placed at controlled distances from the edge and thus they were not capable of

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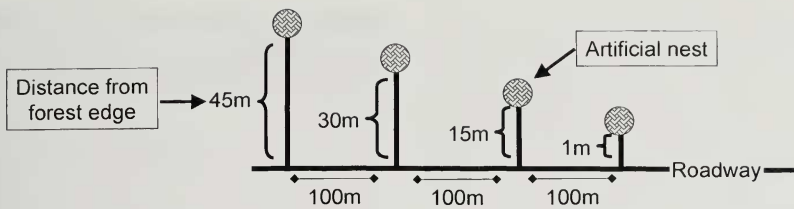


FIG. 1. Schematic of artificial nest placement, northeastern Alabama, 1997. Black lines show the path walked by the researcher when laying each nest. This protocol reduced the probability of predator trap-lining by ensuring that each nest is separated by ≥ 116 m of human trail.

detecting threshold edge effects at small spatial scales.

Murcia (1995) described three types of edge effects: (1) changes in abiotic conditions, (2) direct changes in abundance or distributions of particular species caused by altered abiotic conditions, and (3) indirect changes in abundance or distribution of a particular species as a result of interspecific interactions. In a previous study (Keyser et al. 1998), I suggested that changes in large predator activity (direct biotic effect of fragmentation) increased the predation pressure on songbirds in small forest fragments (indirect biotic effect). However the design of the first experiment did not permit a robust test for edge effects. The current study is designed to circumvent experimental design problems described by Murcia (1995) and Paton (1994) and provide a strong test for edge effects on nest predation rates. Specifically, I tested for an effect of surrounding landscape matrix (forested or developed edge type) and distance from edge on predation of artificial nests.

STUDY AREA AND METHODS

The study was conducted at Fort McClellan (33° 42' N, 85° 45' W) in northeastern Alabama at the southern end of the Appalachian region. I identified three large forest fragments (457, 586, and 849 ha; all mature mixed pine-hardwood); for detailed description see Keyser et al. (1998). Paved roads ≥ 10 m wide with open canopy separated these fragments. They were bordered by developed land consisting primarily of homes or administrative buildings surrounded by lawn. Thus, the study area consisted entirely of large forest fragments, which controls for confounding effects of fragment size and avoids small fragments which could be categorized as all edge (*sensu* Yahner and Wright 1985).

Two types of edge were present: (1) the border between forested and developed land and (2) the roadway border between forest fragments (hereafter referred to as residential edge and forest edge, respectively). The

edge type categorized the landscape matrix in which the edge occurred and was the first treatment in this experiment. The second treatment was distance from edge. Artificial nests were placed in the forest fragment at four distances from the edge (1, 15, 30, and 45 m) in both edge types. The scale of edge effects may vary; however, the metaanalysis by Paton (1994) suggested that most edge effects probably occur ≤ 50 m from edge.

Each artificial nest consisted of a small (about 10 cm in diameter) scrape in the leaf litter and contained two fresh Northern Bobwhite (*Colinus virginianus*) eggs and two eggs (about 12 mm wide) made of gray Plasticine (Roma Italian Plastilina). The fresh eggs provided appropriate visual and olfactory cues to potential predators, and the artificial eggs allowed me to note when small predators, such as mice (*Peromyscus* spp.) and eastern chipmunks (*Tamias striatus*), visited the nest. Mice and chipmunks are unable to damage the relatively large bobwhite eggs (Roper 1992; Haskell 1995a, 1995b), but the use of both bobwhite and Plasticine eggs allowed me to sample effectively the activities of both large and small predators (Donovan et al. 1997, Keyser et al. 1998).

Artificial nest studies provide an index to predation pressures. They can not provide an accurate measure of predation rates on real nests because they do not simulate the nest concealment and nest defense provided by parent birds. Nonetheless, in a study such as this one, they do measure differences in predation risk among treatments.

Since each individual nest was considered an independent sample for this experiment, it was important to minimize the potential for a single predator to trap-line between nests. To this end, I wore gloves while constructing artificial eggs and nests. I walked 100 m along the fragment edge before entering the fragment and walking the appropriate distance to place the nest. I then retraced my steps back to the fragment edge, when possible to a paved road, and paced out or drove another 100 m before entering the patch again to set another nest. The first nest was placed at 1 m, the second at 15 m, the third at 30 m, and the fourth at 45 m from the fragment edge, at which point, the cycle was repeated (Fig. 1). As a result, the human trail from nest to nest was ≥ 116 m. In total, 20 nests per distance interval were laid along the forest edge type, and 17 nests per distance interval were laid along the residen-

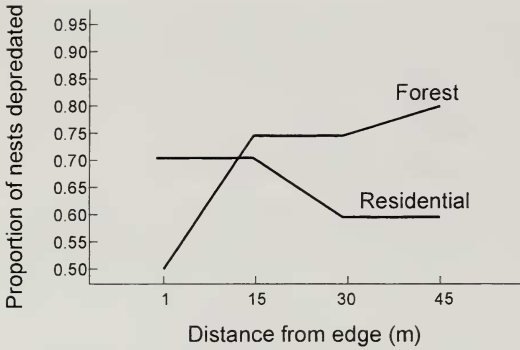


FIG. 2. The proportion of artificial nests depredated in each distance class within the two types of landscape matrix, northeastern Alabama, 1997. For the forest edge type, 10 of 20, 15 of 20, 15 of 20, and 15 of 19 nests were depredated at 1, 15, 30, and 45 m, respectively. For the residential edge type, 12 of 17, 12 of 17, 10 of 17, and 10 of 17 nests were depredated at 1, 15, 30, and 45 m, respectively.

tial edge type. The experiment was set up during the morning on 17 July 1997, and all nests were checked four days later. If any eggs in the nest were damaged, I scored the nest as depredated.

I analyzed these data in two different ways, multiple logistic regression and resampling. For the logistic regression, the response variable was binomial: either the nest was depredated or it was intact. The predictor variables include distance from edge, edge type, and an interaction term. The following model was fit:

$$\ln \left[\frac{p_i}{1 - p_i} \right] = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 (x_1 \times x_2),$$

where p_i is the probability of depredation on any given nest, x_1 is distance from edge, x_2 is edge type, and $x_1 \times x_2$ is the interaction effect (Neter et al. 1996). I used this model to test the hypothesis that predation events depended on location of the nest relative to fragment edge and landscape matrix against the null hypothesis that predation events were stochastic. Initial model fitting and calculation of Wald chi-squared statistics for parameter estimates were performed with SAS 6.09 (SAS Institute, Inc. 1998). Model fit diagnostics including the Hosmer-Lemeshow fit statistic and an index plot of deviance residuals were calculated using SPSS 10.0 (SPSS, Inc. 1999). Pearson residuals and examination of linearity of the logit for distance from edge were performed on a spreadsheet.

Graphical inspection of the data (Fig. 2) suggested that there was an interaction between distance from edge and edge type, but that the effect of distance from edge within edge type was weak. Thus, the three-parameter logistic model may not be the most appropriate way to detect the interaction effect in the absence of strong main effects. As an alternative statistical test, I used resampling to analyze the interaction between distance from edge and edge type. The resampling ap-

proach has several strengths. First, the researcher can define a test statistic that is appropriate for the particular question at hand. Second, the test is free from assumptions about the distribution of the test statistic (Manly 1997).

I calculated the test statistic in the following manner. For each combination of distance from edge and edge type (eight treatment combinations in total), I calculated the predation rate. Next, I calculated the Pearson correlation coefficient between distance from edge and predation rate for each edge type separately and then calculated the difference between the two correlation coefficients ($r_{\text{residential}} - r_{\text{forest}}$), which I refer to as the difference coefficient. To test for significance of the difference coefficient, I randomized nest fate (depredated or intact) with respect to distance from edge within each edge type and calculated the Pearson correlation coefficient for the randomized data. For example, within the forest edge type, there were 80 experimental nests, 20 per distance class. Once the nest fates were assigned randomly, there were still 20 nests per distance class, but the proportion depredated in each distance class was randomly generated. After the correlation coefficients were calculated for each edge type, I calculated the difference coefficient. This was repeated 10,000 times to generate a frequency distribution against which to compare the test statistic calculated from the real data. I performed the randomization and calculated the correlation coefficients and difference coefficients in a spreadsheet using a Visual Basic program kindly provided by Dr. D. Hoyt (program available upon request).

To determine the significance of the test statistic calculated from the actual data, I sorted the 10,000 difference coefficients calculated via randomization and noted the number of random values that exceeded the absolute value of the test statistic. This enabled me to calculate the probability that a value larger than the test statistic would be obtained through random chance.

RESULTS

Overall predation of artificial nests was high (67%, 99 of 147 nests depredated). From Plasticine eggs, I was able to identify some of the predators, and they included mice, birds, deer (*Odocoileus virginianus*) and fox or raccoons (*Procyon lotor*). However, the predator at most (59%) depredated nests was unidentifiable because both bobwhite and Plasticine eggs had been removed from the nest.

The effect of distance from edge on predation rates appeared to differ among edge types (Fig. 2). In general, predation was highest at 1 m and 15 m when the fragment was bordered by residential development. In a forested matrix, predation was lower at 1 m and higher 15–45 m within the fragment. As quan-

tified by logistic regression, the statistical significance of this pattern was not strong. Logistic regression analysis resulted in the following model:

$$\ln \left[\frac{p_i}{1 - p_i} \right] = 0.224 + 0.029x_1 + 0.712x_2 - 0.043(x_1 \times x_2).$$

The overall model was nonsignificant ($\chi^2 = 4.76$, $df = 3$, $P = 0.19$) as were the estimates for β_0 ($\chi^2 = 0.32$, $P = 0.57$), β_1 ($\chi^2 = 3.34$, $P = 0.068$), and β_2 ($\chi^2 = 1.41$, $P = 0.23$). However, the estimate for β_3 , the coefficient for the interaction term, approached significance ($\chi^2 = 3.76$, $P = 0.053$). This suggested that the interaction effect between distance from edge and edge type may have been a more important determinant of predation patterns than simple main effects.

The results of the Hosmer and Lemeshow test showed that this analysis was appropriate for these data ($\chi^2 = 1.40$, $P = 0.97$). Using ungrouped data (all data points equal to either 0 or 1), I calculated deviance residuals and generated an index plot (Neter et al. 1996). This approach revealed no obvious outliers. Using grouped data (predation rate in each of eight distance from edge by edge type groups), I calculated Pearson residuals. When plotted against the predicted predation rate, the residual plot was ambiguous because there were only eight data points. Similarly, it was difficult to assess the linearity of the logit transformation for distance from edge because this required calculating the predation rate for each group, which reduced the sample size to four per edge type. However, I plotted the logit of predation rate, $\ln(p/q)$, against distance from edge for each edge type. Visual inspection of the plot showed no obvious deviations from linearity, although linear regression analyses were nonsignificant (forest edge: $r^2 = 0.72$, $F = 5.23$, $P = 0.15$; residential edge: $r^2 = 0.81$, $F = 8.27$, $P = 0.10$). I attributed the lack of significance to the degrees of freedom ($df = 3$), not to a lack of linearity.

The resampling approach was sensitive enough to detect the interaction using the difference coefficient statistic ($r_{\text{residential}} - r_{\text{forest}}$). There was a nonsignificant, negative correlation between distance from edge and predation rate in the residential edge type ($r =$

-0.897 , $P = 0.10$). In the forested edge type, the correlation was positive and also nonsignificant ($r = 0.835$, $P = 0.17$). The lack of significance in these two correlations was attributable to the reduction in degrees of freedom that occurred when I calculated predation rate for each distance from edge by edge type combination, but also was reflective of weak main effects as revealed by the logistic regression analysis. However, the resampling approach allowed me to document the interaction effect between distance from edge by edge type more convincingly. The difference coefficient calculated from the real data was significant when tested via resampling (difference coefficient = -1.732 , $P = 0.018$). The difference coefficient quantified the difference in nest predation trend between forested and residential edge types and suggested that edge type influenced whether the relationship between distance from edge and predation rate was negative or positive. This result suggested that the interaction between distance from edge and edge type was the most meaningful biological pattern detected in the experiment.

DISCUSSION

Data from point counts conducted in my study area suggest that many Neotropical migrant songbird species no longer breed in small forest fragments (Soehren 1995). In a previous experimental study, we observed changes in predator activity with forest fragmentation and concluded that increased nest predation intensity may, in fact, be a potential cause of songbird population decline (Keyser et al. 1998). This study provides more supporting evidence. Nest predation patterns in the study area appear to be associated with distance from edge and the type of landscape surrounding the forest patch. The potential effect of forest fragmentation on nesting songbirds depends upon the interaction between these two variables. An accurate assessment of nest predation dynamics requires consideration of this interaction. It is possible that edge-related changes in predator activity or community composition are driving the pattern observed in this study. This is especially likely to be the case if predator species respond differentially to the surrounding landscape matrix.

Many previous studies have looked for

edge effects on nest predation rates in both natural and experimental designs. However, previous results have been equivocal. Paton's (1994) review of the literature found that 14 of 21 studies documented increased predation rate near edges. A metaanalysis by Söderström et al. (1998) found increased predation on nests <50 m from edge relative to nests deeper in the forest fragment. However, only about half of the studies that looked for edge effects found them. In these studies, researchers did not control for the effects of the landscape matrix in which fragments were embedded. This might explain the disparity of results.

The edge effects observed in this study would have been obscured had I not controlled for edge type. My results are consistent with a number of other studies. A review by Andrén (1995) suggested that edge effects on nest predation occurred in forest fragments embedded in an agricultural landscape but not in a forested landscape (see also Bayne and Hobson 1997). My result supports a metaanalysis by Hartley and Hunter (1998) that showed a trend toward increased edge-related predation only in deforested landscapes (both studies in deforested landscapes found edge effects, but only 3 of 13 in a forested context showed edge-related increases in predation).

A complete understanding of nest predation dynamics in ecotones depends upon many factors. Species specific habitat use, nest placement or concealment, and nest defense all can influence nest predation patterns (Pasitschniak-Arts et al. 1998, Restrepo and Gómez 1998). In addition, predator specific, edge-related predation has been shown in several studies (Pasitschniak-Arts and Messier 1996, Arango-Velez and Kattan 1997, Bayne and Hobson 1997). Understanding the behavioral patterns of nesting birds and potential predators relative to the abiotic characteristics of ecotones will facilitate a deeper understanding of edge effects.

Although the pattern was somewhat weak, my study found evidence for an interaction between distance from edge and edge type that influenced nest predation patterns on small spatial scales. Further study clearly is warranted to determine if the same pattern holds in other locations, and if so, to deter-

mine the underlying cause of differential nest predation.

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